TRANSOCEANIC MIGRATION OF THE BLACKPOLL WARBLER: SUMMARY OF SCIENTIFIC EVIDENCE AND RESPONSE TO CRITICISMS BY MURRAY

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Abstract.—The hypothesis that Blackpoll Warblers (Dendroica striata) make transoceanic flights in autumn from the northeastern U.S. and southeastern Canada to South America has been proposed or supported in more than 25 papers by many authors, using many techniques. Murray (1989; unpubl.) has criticized this hypothesis, but cited only a few of these papers and misrepresented much of the information that he did cite. Murray misstated information on the location of the western fringe of the SSE flights, the importance of misidentifications, and the phenology of departures. Murray's comparison of regional mean masses was invalid, because the data sets were heterogeneous and non-comparable. Contra Murray, all radar studies in the area have reported directed flights of birds identified as songbirds towards the SSE over the western North Atlantic Ocean, Under Murray's alternative hypotheses, the entire continental population of the species would be concentrated into the coastal plain of the southeastern U.S., but he has cited only two specific records for this entire area. The general statements of status that he cited are outdated, unreliable, and/ or undocumented. In contrast, Nisbet (1970a) and McNair and Post (1993a) cited numerous published and unpublished records for this area, including McNair and Post's own extensive field work. These data show that the species is scarce to rare in this area, decisively refuting Murray's hypotheses.

MIGRACIÓN TRANSOCEÁNICA DE DENDROICA STRIATA; RESUMEN DE INVESTIGACIONES Y RESPUESTA A LA CRÍTICA DE MURRAY

Sinopsis.—La hipótesis de que *Dendroica striata* lleva a cabo vuelos transoceánicos en el otoño desde el noreste de los Estados Unidos y el sureste del Canadá hasta América del Sur, ha sido propuesta o apoyada por diferentes autores de más de 25 artículos, que han utilizado diferentes técnicas. Murray (1989; manuscrito sin publicar) sólo cita algunos de estos trabajos sin ofrecer una representación adecuada de toda la información disponible. Éste además no

interpreta, adecuadamente, información referente a la localización del margen occidental de los vuelos sur-sureste, la importanica de las identificaciones erróneas y la fenología de partida. La comparación de Murray de las masas corporales promedios en las diferentes regiones es inválida debido a que el conjunto de datos es heterogéneo y por ende no comparable. En contra de Murray están los estudios de radar que han documentado vuelos directos de paseriformes hacia el sur-sureste sobre la parte occidental del Atlántico Norte. Bajo lo hipótesis alterna de Murray, la población continental en su totalidad estaría concentrada en la llanura costanera del sureste de los Estados Unidos, pero él sólo cita dos registros en particular para toda el área. Las citas que utiliza para determinar el estatus de las aves en las diferentes localidades son muy viejas, poco confiables y/o sin documentar. En contraste, Nisbet (1970a) y McNair y Post (1993a) citan numerosos registros publicados y sin publicar para el área, incluyendo el extensivo trabajo de campo de McNair y Post. Estos datos demuestran que la especie es escasa a rara y refutan decisivamente la hipótesis de Murray.

During autumn migration, Blackpoll Warblers (Dendroica striata) are concentrated in the northeastern United States and in southeastern Canada (Nisbet 1970a). Several authors have presented evidence for the hypothesis that most Blackpoll Warblers then make long transoceanic flights to the West Indies and northern South America (McNair and Post 1993, Nisbet 1970a, Nisbet et al. 1963, Williams and Williams 1978, Williams et al. 1977). This hypothesis has been widely cited and appears to be widely accepted, but has been criticized repeatedly by Murray (1965, 1989, unpubl.), who claims that Blackpoll Warblers instead migrate via the southeastern U.S. We originally prepared this paper in response to Murray (unpubl.—Transoceanic migration of the Blackpoll Warbler: separating fact from fiction), but Murray withdrew that critique from publication after seeing our response. This paper now serves two purposes. First, we summarize the scientific evidence for the hypothesis of transoceanic migration, which has been published in many different papers and has not previously been presented in a unified way. Second, we respond to the arguments by Murray (1989), many of which were repeated or cited by Murray (unpubl.).

SUMMARY OF EVIDENCE FOR THE HYPOTHESIS OF TRANSOCEANIC MIGRATION

The hypothesis that Blackpoll Warblers make transoceanic migrations in autumn is referred to here as the "multi-author hypothesis" (MAH), because many authors have proposed it and/or provided evidence in support of it. The main lines of evidence favoring the MAH are the following.

1. Observations with radar (Drury and Keith 1962; Drury and Nisbet 1964; Ireland and Williams 1974; Larkin 1991; Larkin et al. 1979; Mc-Clintock et al. 1978; Nisbet and Drury 1967; Nisbet et al. 1963; Williams 1985; Williams and Williams 1978a, 1978b, 1990a, 1990b; Williams et al. 1974, 1977; Richardson 1972, 1975, 1976, 1980) and by moon-watching (Nisbet and Drury 1969) of large numbers of songbirds departing from Virginia, Massachusetts, and Nova Scotia towards the SSE, passing Bermuda in a SE direction, and passing over Puerto Rico and the Lesser Antilles in a SSW direction. Although many of these papers reported observations from only one or a few locations, Williams and his colleagues used a network of radar facilities throughout this area and were able to

track movements of songbirds sequentially across the entire western North Atlantic Ocean (Williams and Williams 1978a, Williams et al. 1977).

- 2. Data from nocturnal accidents, systematic mist-netting, and surveys of grounded migrants, showing that Blackpoll Warblers are concentrated on autumn migration between Virginia and Nova Scotia, and are scarce to rare southwest of northeastern North Carolina, except for sporadic occurrences of grounded migrants along the coast or nocturnal accidents (McNair and Post 1993a, Nisbet 1970a).
- 3. Observations of songbird migrants passing Bermuda, Puerto Rico and the Lesser Antilles without landing (Ireland and Williams 1974, Nisbet et al. 1963, Richardson 1976, Williams and Williams 1978a, Wingate 1973).

Although these lines of evidence have been developed independently, by different methods, and at different locations, they have been linked in several publications (Nisbet 1970a; Nisbet and Drury 1967, 1969; Nisbet et al. 1963; Richardson 1980; Williams and Williams 1978a). In particular, these publications link the transoceanic movements of songbirds that have been tracked using radar with departures, passage, and arrivals of Blackpoll Warblers. Some birds passing Bermuda without landing were identified as Blackpoll Warblers (Nisbet et al. 1963, Wingate 1973).

Other sets of data that are consistent with or support the MAH include data on phenology (Nisbet 1970a), pre-migratory fattening and in-flight fat condition (Cherry et al. 1985, McNair and Post 1993a, Murray 1989, Nisbet et al. 1963), rates of mass loss (Hussell and Lambert 1980, Nisbet et al. 1963), banding recoveries (Hall 1983, Nisbet 1970b, Walkinshaw 1976), age ratios (Murray 1966b, 1979; Nisbet et al. 1963; Ralph 1975), other differences between coastal and inland stations (Nisbet 1970a; Nisbet and Drury 1967, 1969; Nisbet et al. 1963), occurrences on ships (Cherry et al. 1985, McClintock et al. 1978), orientation (Ralph 1975; Stoddard et al. 1983; Williams 1985; Williams and Williams 1978a, 1990a, 1990b), and flight times (Williams and Williams 1978b, Williams et al. 1978).

Of the 32 papers that have been cited in this section as providing the basis for the MAH, Murray (1989) cited only 15, including two of his own; Murray (unpubl.) cited only nine. As documented below, we believe that Murray selectively cited or misrepresented several of the papers that he did cite. Accordingly, most of Murray's criticisms of the MAH were misconceived or misdirected.

MURRAY'S HYPOTHESES

Murray has proposed two different hypotheses, which we refer to as M1 and M2.

M1. Murray (1965, 1966a), following and citing Cooke (1904, 1915), proposed that Blackpoll Warblers migrate first ESE to the northeastern USA, then SW down the coast to Georgia and Florida, then SE towards their winter quarters in northern South America. Figure 1 in Murray (1966a) illustrated this hypothesis.

M2. Murray (1989) modified M1 to eliminate the hypothesis that Blackpoll Warblers concentrate in the northeastern U.S. before migrating southwest, and to place the departure area further to the northeast. "It now seems more likely that Blackpoll Warblers funnel from the breeding range to the southeastern United States, along with the general movement of migration (Gauthreaux 1980), and depart from somewhere between Cape Hatteras and northern Florida" (Murray 1989:8). Figure 1 in Murray (1989) illustrated this hypothesis. Murray cited no specific data in support of either hypothesis, and gave no reasons for changing M1 to M2.

WESTERN LIMITS OF TRANSOCEANIC FLIGHTS

Nisbet (1970a) showed that the area where Blackpoll Warblers are concentrated in autumn extends southwestwards at least as far as northern Virginia and eastern West Virginia (about 80°W). Hall (1983) further documented the abundance of the species in West Virginia. Nisbet (1970a) showed that several occurrences of small to moderate numbers of Blackpoll Warblers in Florida, in the Bahamas, and probably in South Carolina coincided exactly with storms, "suggesting disruption of migration" (Nisbet 1970a:228). Nisbet (1970a) further stated "Table 5 suggests that the southwestern limit of large numbers is in the region of Cape Hatteras, but critical data are lacking for this region and it is likely that there is no sharp boundary.... On the western margin of the flights, some birds must pass within 100 miles of southern Florida..." (Nisbet 1970a:228, emphases added).

Murray (1989, unpubl.) claimed to find inconsistencies in these statements, but miscited and misrepresented them. Figure 2 in Murray (1989) misrepresented the MAH by showing all Blackpoll Warblers departing from east of Cape Hatteras and some flying southwest towards the Bahamas, contradicting the passage quoted above. Murray (unpubl.) misrepresented the MAH by stating that that the Blackpoll Warblers that occur in the southeastern USA "are supposed to be flying more than 1,000 km east of Florida."

STATUS IN THE SOUTHEASTERN UNITED STATES

Murray (1989, unpubl.) cited several general statements about the status of Blackpoll Warblers in the southeastern United States in support of his hypothesis that "Blackpoll Warblers migrate through the coastal southeastern United States in the fall." There is no dispute that *some* Blackpoll Warblers occur along the coast of the southeastern United States in the fall (Nisbet 1970a, McNair and Post 1993a, and refs. therein). Occurrences in north central and northeastern North Carolina (including the Outer Banks; Sykes 1986) are not at issue, because Blackpoll Warblers migrate through these areas under all three hypotheses. Occurrences in most of Florida are not at issue, because Nisbet (1970a) found that most records there were of birds brought in from the east by storms with northeast winds, and Murray (1989:12) concurred with this finding. Occur-

rences far inland in South Carolina and Georgia are not at issue, because Nisbet (1970a) and McNair and Post (1993a) showed that the species is scarce to very rare in these areas; Murray did not dispute this and M2 limits the departure area to the "coastal plain" (Murray 1989:10). The area for which there is dispute, therefore, can be narrowed to the coast and coastal plain from southeastern North Carolina to northeastern Florida. Under the MAH, the western fringe of the transoceanic migration passes over this area (see previous section), so that some occurrences of Blackpoll Warblers there may be fallout from that fringe; others may be of birds diverted westwards by storms, as in Florida and the Bahamas (Nisbet 1970a:226), and/or stragglers. Under M1 or M2, however, this area is supposed to be the staging area for the entire North American population. Hence, the density of grounded birds in this area would have to be much higher than that in areas to the northeast (e.g., West Virginia to Massachusetts), because much larger numbers of birds would be concentrated into a much smaller area. Nisbet (1970a) and McNair and Post (1993a) showed that this is not the case; indeed, the reverse is true.

Murray (1989, unpubl.) did not cite any actual records of Blackpoll Warblers from his supposed area of departure; instead, he relied on six general characterizations of its status there. First, he selectively cited from Nisbet (1970a), who characterized the species as "Common: 5% of netted warblers in N" in coastal North Carolina, and "Fairly common: 3% of netted warblers; 0.1% of warbler kills" in coastal South Carolina (Table 5, emphases added). Murray failed to cite the italicized phrases, and ignored the rest of this table, which characterized the species as scarce or rare in coastal Georgia and scarce to very rare inland in all three states, but much more numerous in areas to the north and northeast. The information on which Nisbet based this table has been updated by McNair and Post (1993a), whose characterizations supersede those of Nisbet. Specifically, McNair and Post reviewed extensive data for South Carolina, including the limited data available to Nisbet (1970a), and concluded that the species is rare in the state in autumn, even on the coast.

Of the remaining sources cited by Murray, Potter et al. (1980) is a popular book without scientific documentation; the statement that Blackpoll Warblers are "uncommon to fairly common" did not distinguish between North and South Carolina and hence contributes nothing to resolving the dispute. Burleigh (1934, 1958) stated that the species is "common only on the coast" of Georgia in the fall and "is then merely a straggler in the interior of the state." Burleigh cited only two actual records on the coast, however, and gave no basis for his statements about its status there. As he himself (Burleigh 1934) showed that earlier statements about its status inland were erroneous because of misidentifications, his claim that it was "common" on the coast cannot be accepted without any documented basis; it conflicts with more recent data (see next paragraph). This issue was discussed by both Nisbet (1970a) and McNair and Post (1993a). Kale and Maehr (1990) is a popular book without scientific documentation; their statement that the species is "uncommon"

in Florida is not specific to the area in dispute. Denton et al. (1977) stated that the species is a "rare fall transient over most of [Georgia]"; contra Murray (1989, 1995), this statement is inconsistent with M1 and M2.

Murray (unpubl.) failed to cite the most recent and most definitive references on the status of birds in these states: South Carolina (McNair and Post 1993b, Post and Gauthreaux 1989); Georgia (Haney et al. 1986); Florida (Robertson and Woolfenden 1992, Stevenson and Anderson 1994). Except for Haney et al. (1986), each of these five publications is fully documented, and the information summarized in each is inconsistent with M1 and M2.

Despite promoting M1 and M2 over a 30-yr period, Murray (1965, 1966a, 1989, unpubl.) has not yet cited a single first-hand report of a Blackpoll Warbler in southeastern North Carolina, South Carolina, or Georgia; the only two records he has cited for Florida (Case et al. 1965, Roberts and Tamborski 1993) were of birds killed in nocturnal accidents, not grounded migrants. In contrast, Nisbet (1970a) and McNair and Post (1993a) cited numerous published and unpublished records from nocturnal accidents, systematic mist-netting, and field surveys. Together, McNair and Post have 45 years' field experience in these states, including mist-netting more than 25,000 autumn migrants since 1983. All this information shows that the species is scarce to rare in the exact areas where the species would be concentrated under M1 or M2; hence, it decisively refutes these hypotheses.

MISIDENTIFICATIONS

Murray (unpubl.) claimed that "McNair and Post (1993), as well as Nisbet (1970a), hypothesize that most reports of Blackpoll Warblers in the southeastern United States are based on misidentifications. They dismiss reports of Blackpoll Warblers in the southeastern United States . . . there is no evidence whatsoever of wholesale misidentification of warblers by southerners ... the hypothesis of a transoceanic flight relies on the assumption that bird watchers in the southeastern states misidentify birds." All these statements are false. Nisbet (1970a) cited several published and unpublished reports of widespread misidentification of Dendroica warblers by southerners, and consequently ignored records published prior to 1934, plus undocumented general statements such as that of Burleigh (1958; see previous section). McNair and Post (1993a) also discussed problems of misidentification in the past. Nevertheless, both Nisbet (1970a) and McNair and Post (1993a) cited, tabulated, and relied on many reports of Blackpoll Warblers in the southeastern states since the 1930s. The MAH does not rely on the assumption that any or all of these birds were misidentified.

TIMING OF MIGRATION

Murray (unpubl.) stated "We know that Blackpoll Warblers migrate through New England and New Jersey from early September through the first week of October.... If Blackpoll Warblers are departing New England and crossing the ocean throughout September, why are they not found in their greatest numbers at Bermuda, the Bahamas ... and the Caribbean in September?" These statements misrepresent both the available data and the MAH. In this section of his commentary, Murray failed to cite Nisbet (1970a), who presented a quantitative analysis of the phenology of Blackpoll Warblers at 10 banding stations from Virginia and West Virginia to Maine (Nisbet's Table 4). Except for one station in Maine, median dates of occurrence were between 24 September and 5 October, and third quartile dates were between 28 September and 13 October: birds were encountered in numbers at inland stations until 20 October and at coastal stations until 30 October. Under the MAH, the period before the median date is interpreted as a period of arrival, dispersal, and pre-migratory fattening (Nisbet 1970a, Nisbet et al. 1963), and the main period of departure across the ocean is identified as between 24 September and 20 October, not "throughout September." The period of arrival and maximum numbers of Blackpoll Warblers in Bermuda and the Lesser Antilles exactly coincides with this range of dates, allowing 1-3 d for transit and a variable period for stopover (Nisbet 1970a, Pashley and Hamilton 1990, Wingate 1973).

GEOGRAPHIC VARIATION IN MASS

Murray (1989, unpubl.) claimed that the pattern of variation in mean mass of Blackpoll Warblers—"lowest in the north (Michigan, New Jersey, and Massachusetts), greatest in Florida, and intermediate at Bermuda" is inconsistent with the MAH. The comparison of mean masses is unscientific and meaningless, however. The birds weighed in Florida were intercepted while migrating at night (Murray 1989), those weighed at Bermuda were a mixture of birds intercepted while migrating at night and grounded migrants (Nisbet et al. 1963), those weighed in New Jersey were short-stay transients on the coast (Murray 1979), and those weighed in Massachusetts were a mixture of arriving, dispersing, and fattening birds (Nisbet et al. 1963). Hence, the mean masses are not comparable among these groups. Nisbet et al. (1963) presented a detailed analysis of day-today changes in mean and individual masses, showing that most birds passed through their banding stations at low mass, while some remained and deposited fat, departing in October at masses much higher than those recorded for in-flight transients at Bermuda. When scientifically assessed and properly cited, the data on masses are fully consistent with and provide strong support for the MAH.

RADAR AND OBSERVATIONS AT SEA

Murray (1989) stated that "no southward or southeastward departures have been tracked from New England to the Caribbean or South America." Murray (unpubl.) stated that "radar has not found a directed movement of passerine migrants over the ocean." These statements are patently false. Williams and Williams (1978a) described in detail the tracking of a wave of migrants from Cape Cod (among other departure points)

past Bermuda to Puerto Rico, Antigua, Barbados and Tobago. Numerous radar studies have shown directed movements of passerine migrants over the western North Atlantic Ocean, whether departing SSE from the continent, passing SE through the area of Bermuda, continuing SE over the open ocean, or arriving in the West Indies from the NNE (see refs. listed above under point 1). All observers who have used radars on ships at sea detected directed flights of small, relatively slow-flying birds moving S or SE towards the Caribbean and South America, as well as some disoriented birds flying in the vicinity of weather fronts (Larkin 1980, 1991; Larkin et al. 1979; McClintock et al. 1978; Williams and Williams 1978b; Williams et al. 1974). The disoriented flights were associated with passerine species wintering in North America, whereas directed flight behavior was associated with species wintering in the Caribbean and South America (Williams and Williams 1978b). Murray (1989, unpubl.) ignored the many observations of directed flights and cited only papers by Larkin et al. (1979) and Larkin (1980). Larkin (1991), however, re-evaluated his earlier work and concluded that many of the poorly-oriented targets were insects, not birds. After removing the insect tracks, Larkin concluded that his data "provide strong retrospective support for the hypothesis of Williams and Williams (1978) that transoceanic migrant birds maintain a nearly constant SE heading. Many flight speeds can be attributed to small warblers, contra Murray (1989)." In view of this published correction, it is incomprehensible that Murray (unpubl.) again cited Larkin's earlier papers for the proposition that radar has not detected directed movements of passerine migrants over the ocean.

EXTRAORDINARINESS

Murray (unpubl.) asserted that "The implications of [the MAH] for our knowledge of avian physiology, navigation, and migratory behavior are so great that ornithologists should make every effort to document this extraordinary migration route." Although we agree with the need for more study and hope that it will be performed, we do not agree that the transoceanic migration of the Blackpoll Warbler is undocumented, nor that it is as "extraordinary" as stated. Transoceanic migrations have been reported for many species (e.g., Williams et al. 1990a, 1990b). That of the Blackpoll Warbler is one of the longest and best documented for a songbird, but it is not unique or exceptional. For example, the migration of the Greenland Wheatear (*Oenanthe oenanthe*) from North America to and from Europe (Cramp 1988, Snow 1953) is as long and probably as demanding, especially in spring.

In contrast, we believe that the migration patterns proposed in M1 or M2 would be extraordinary and would need detailed documentation. They would require many or most individuals of the species to perform a zig-zag migration: SE or ESE to the northeastern U.S., then SW to the southeastern U.S., then SE again to the winter quarters. The second and third legs of this hypothetical route would almost double the distance to be travelled from Nova Scotia to northern South America, and would

sacrifice the advantage gained from favorable winds during the overwater crossing (Williams et al. 1977, 1978). The third leg of this hypothetical route would require a long overwater flight against the prevailing winds. As illustrated in Figure 1 of Murray (1989), M2 would require a *transoceanic* flight almost as long and at least as "extraordinary" as that proposed under the MAH.

Furthermore, if the large numbers of songbirds seen departing SSE from New England and Nova Scotia and tracked across the ocean to the Lesser Antilles and South America in early October (Drury and Nisbet 1964; Nisbet and Drury 1969; Nisbet et al. 1963; Richardson 1972, 1980; Williams and Williams 1978a, 1978b) were not Blackpoll Warblers, what could they have been? The density of birds in some of these departures was estimated to be in the range 300–700 km⁻² (Nisbet 1963; Nisbet et al. 1963; Nisbet and Drury 1967, 1969). Although Blackpoll Warblers were as abundant as this in New England in the 1960s, we know of no other species that was similarly abundant—certainly no other species that winters in South America (Nisbet and Drury 1967). Thus, acceptance of M1 or M2 would imply extraordinary behavior in some other species.

SCIENTIFIC METHOD

Murray (unpubl.) urged that a clear distinction be made between facts and hypotheses ("what we know and what we imagine about the post-breeding migration of the Blackpoll Warbler"). We agree that the MAH is an hypothesis (or set of hypotheses) about the migration of the Blackpoll Warbler. Likewise, M1 and M2 are alternative hypotheses about the same migration. All three claim to explain the same facts (although the MAH is based on a much more extensive set of data). Absent some technical breakthrough in tracking individual birds, it is unlikely that the differences between MAH and M1 or M2 will be resolved by direct observation. Hence, choice between the hypotheses must be based on interpretation of indirect observations.

Since the MAH was first formulated by Drury and Keith (1962) and Nisbet et al. (1963) and challenged by Murray (1965), much additional information of many different types has been generated (see the section SUMMARY OF EVIDENCE FOR THE HYPOTHESIS OF TRANSOCE-ANIC MIGRATION at the beginning of this commentary). We believe that all this evidence is consistent with the MAH, and that some of the evidence strongly supports it. In contrast, M1 and M2 have not been supported by any new or independent evidence, and both failed their first tests (Nisbet 1970a, McNair and Post 1993a, respectively). Murray's (unpubl.) belief that the ornithological community appears to have accepted the MAH and to have ignored M1 and M2 may be justified, but this outcome reasonably reflects the weight of scientific evidence.

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